

## Security areas for elk during archery and rifle hunting seasons

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### Abstract:

Fall elk (*Cervus canadensis*) habitat management on public lands provides security areas for reasonable elk survival and hunter opportunity. The management focus of maintaining or improving security areas, combined with conservative harvest regulations, may explain why some elk populations have increased in the western United States. However, in areas that include lands that restrict public hunter access, elk may alter their space use patterns during the hunting season by increasing use of areas that restrict public hunter access rather than using security areas on adjacent public lands. We used global positioning system location data from 325 adult female elk in 9 southwest Montana populations to determine resource selection during the archery and rifle hunting seasons. We found that during the archery season, in order of decreasing strength of selection, elk selected for areas that restricted access to public hunters, had greater time-integrated normalized difference vegetation index values, had higher canopy cover, were farther from motorized routes, and had lower hunter effort. During the rifle season, in order of decreasing strength of selection, elk selected for areas that restricted access to public hunters, were farther from motorized routes, had higher canopy cover, and had higher hunter effort. Interactions among several covariates revealed dependencies in elk resource selection patterns. Further, cross-population analyses revealed increased elk avoidance of motorized routes with increasing hunter effort during both the archery and rifle hunting seasons. We recommend managing for areas with  $\geq 13\%$  canopy cover that are  $\geq 2,760$  m (1.7 miles) from motorized routes, and identifying and managing for areas of high nutritional resources within these areas to create security areas on public lands during archery season. During the rifle season, we recommend managing for areas with  $\geq 9\%$  canopy cover that are  $\geq 1,535$  m (0.95 mile) from motorized routes, and are  $\geq 20.23$  km<sup>2</sup>. Lastly, given increased elk avoidance of motorized routes with higher hunter effort, we recommend that to maintain elk on public lands, managers consider increasing the amount of security in areas that receive high hunter effort, or hunting seasons that limit hunter effort in areas of high motorized route densities.

In addition to their ecological impacts on vegetation and plant community structure (Hobbs [1996](#); Wolf et al. [2007](#); Marshall et al. [2014](#), [2013](#)), elk (*Cervus canadensis*) provide important cultural and economic benefits to much of the western United States through tourism and hunting (Duffield and Holliman [1988](#)). In many western states, the majority of elk hunting occurs on public lands, highlighting the need for wildlife managers and public land managers to cooperatively manage elk habitat. Traditional fall elk security area management on public land is based on managing motorized routes and hiding cover. This concept was first formalized by Hillis et al. ([1991](#)) based on work conducted during the rifle hunting season on elk that occupied relatively continuous conifer forests in western Montana. The objective of managing for security areas was to provide a reasonable level of male elk survival during the rifle hunting season while still allowing for hunter opportunity. Hillis et al. ([1991](#)) recommended to manage for contiguous cover blocks  $\geq 1.01$  km<sup>2</sup> that are  $\geq 0.80$  km from the nearest motorized route, though the requirements for block size and distance to the nearest motorized route were not considered to be an exact recipe to be followed in all situations. As such, a variety of security definitions, some including specific requirements for canopy cover, are commonly implemented in national forest

management plans (Christensen et al. [1993](#)). The relative importance of canopy cover for elk security areas has been questioned, especially in areas with less dense forest cover (Montana Department of Wildlife and Parks [MDFWP] and U.S. Department of Agriculture [USDA] Forest Service [2013](#)), but has not been formally evaluated.

Extrapolations of traditional security area parameters to less densely forested habitats, mixed ownership regions, archery hunting seasons, and female elk survivorship may not be valid. In areas that include a matrix of publicly accessible and restricted access lands, elk may decrease their use of security areas (Hillis paradigm) on public lands and increase their use of areas that restrict public hunter access during the hunting season (Burcham et al. [1999](#); Conner et al. [2001](#); Hayes et al. [2002](#); Proffitt et al. [2010](#), [2013](#)). Additionally, in many areas, hunting seasons are designed to decrease the number of elk, and as such are focused on increasing the harvest of adult female elk rather than solely on maintaining male elk survival. If female elk are not available to hunters in sufficient numbers because of a distribution shift from publicly accessible to restricted access lands, then harvest is not an effective tool to reduce adult female survival and overall elk population growth. Elk distribution shifts from publicly accessible to restricted access lands, whether the result of short-term changes in hunting pressure (Millspaugh et al. [2000](#), Proffitt et al. [2010](#)) or long-term behavioral adaptations (Boyce [1991](#)), is a major challenge to wildlife and land managers as they attempt to maintain elk populations at socially acceptable levels while also meeting public demand for hunting opportunities (Haggerty and Travis [2006](#)).

The timing and degree of changes in elk distributions during hunting season are not consistent across populations; some populations show little to no change in distribution across publicly accessible and restricted access lands during the hunting season, or even increase use of publicly accessible areas during the hunting seasons. This may be the result of a functional response in resource selection (Mysterud and Ims [1998](#), Mabile et al. [2012](#)), where the strength of selection for or against publicly accessible or restricted access lands is dependent on the availability of that resource. Each population's annual range comprises different proportions of publicly accessible lands with different levels of hunter pressure. Thus, differences in the strength of selection for various habitat attributes may be related to these differences in hunter access and hunter pressure. Additionally, the effects of the archery and rifle season on elk distributions vary across populations and likely correlate with different degrees of hunting pressure during each season. Some elk populations begin redistribution during the archery season (Conner et al. [2001](#), Vieira et al. [2003](#), Proffitt et al. [2013](#)), whereas others do not respond until the rifle season (Millspaugh et al. [2000](#), Johnson et al. [2004](#), Proffitt et al. [2013](#)), if at all. Differences in hunter pressure during rifle and archery seasons and differences in topography and elk migratory behavior have been suggested to explain the differences among the selections made by different populations (Conner et al. [2001](#), Proffitt et al. [2013](#)).

Although most research and management has focused on the impacts of rifle hunting on elk, archery hunting has been increasing in popularity, with a 98% increase in archery license sales in Montana since 1985 (Montana Fish, Wildlife and Parks, unpublished data). As such, understanding elk responses to archery hunting and incorporating potential archery hunting effects into elk management plans is important. Archery hunting can lead to reduced pregnancy rates and delayed conception in elk (Davidson et al. [2012](#)). Nutritional condition of female elk during the late-summer and rut is also related to pregnancy rates and conception (Noyes et al.

[2004](#), Cook et al. [2013](#)). Human disturbance associated with archery hunting may shift elk distributions away from areas of high nutritional resources, potentially affecting elk population dynamics further than would be expected through archery hunting mortality alone.

We used fine-scale location data collected during 2005–2014 to assess female elk resource selection during the archery and rifle hunting seasons in 9 elk herds in southwestern Montana. We also examined potential functional responses in elk resource selection by comparing the standardized coefficient estimates from population-specific models along gradients of accessible:restricted access lands and mean hunter pressure to determine whether the relative availability of publicly accessible land or population-specific hunter pressure influence the direction or strength of elk resource selection during the hunting seasons. Finally, we evaluated the traditional paradigm of elk security areas (Hillis et al. [1991](#)) against security area metrics derived from our top resource selection function models for archery and rifle hunting seasons.

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The study area included the annual ranges of 9 elk populations in southwestern Montana (Fig. [1](#)). Climate in these ranges is characterized by short, cool summers and long, cold winters. Vegetation types across these ranges included a mix of montane forest (e.g., aspen [*Populus tremuloides*], Douglas fir [*Pseudotsuga menziesii*], lodgepole pine [*Pinus contorta*]), open sage-grassland (e.g., big sagebrush [*Artemisia tridentata*], blue-bunch wheatgrass [*Pseudoroegneria spicata*], Idaho fescue [*Festuca idahoensis*]), and upland grasslands, meadows, and unvegetated areas, but the relative proportions of these vegetation types varied among the populations. All elk ranges included a mix of public lands that are generally accessible to public hunters, primarily managed by the United States Forest Service or Bureau of Land Management, privately owned lands that are accessible to hunters through a State of Montana hunter access program, and privately owned lands with unknown and varying degrees of restrictions on public hunter access. Additionally, several of the herd ranges overlap with Yellowstone National Park, which is public land but no hunting is allowed. Elevation, motorized route densities, and indices of nutritional resources varied among the populations' ranges (Table [1](#)). Mule deer (*Odocoileus hemionus*), white tail deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces americanus*) also occupy the elk ranges. Wolves (*Canis lupus*), mountain lions (*Puma concolor*), American black bears (*Ursus americanus*), and coyotes (*Canis latrans*) are the elk predators in the system, and grizzly bears (*Ursus arctos*) are also found in the ranges in the

eastern portion of the study area. Gude et al. (2006), White et al. (2012), and Proffitt et al. (2014, 2013) provide full descriptions of these areas.

Table 1. The mean and standard deviation (where applicable) of landscape attributes of 9 elk population annual ranges within southwestern Montana, USA, 2005–2014.. The values presented are based on the minimum spatial scale available for each of the covariates

Population	Elevation (m)		Distance to motorized routes (m)		Canopy cover (%)		Time- integrated NDVI <sup>a</sup>		Publicly accessible	Hunter effort (days/km <sup>2</sup> )	
	̄	SD	̄	SD	̄	SD	̄	SD	Proportion	̄	SD
Normalized difference vegetation index.											
Bitterroot East Fork	1,917	329	1,662	1,861	26.4	26	48.3	11	0.77	7.48	4.2
Bitterroot West Fork	1,907	274	1,999	2,204	35.8	23	45.1	8.8	0.96	1.9	0.2
Blacktail	2,200	264	1,831	1,635	14.9	22.6	51	13	0.82	4.85	2.53
Dome Mountain	2,430	282	6,369	5,417	26.2	24.1	53	10	0.19	1.97	4.16
Madison Valley	2,273	356	2,981	2,853	26	25.9	52.1	13	0.62	5.79	3.02
Paradise Valley	2,194	424	3,406	3,070	25	24.1	47.3	12	0.45	8.23	3.10
Pioneers	2,144	286	1,675	1,562	25.8	28.9	44.8	13	0.75	5.91	2.68
Sage Creek	2,177	226	2,408	2,226	10.6	19.7	50.4	13	0.81	4.15	1.37
Sapphires	1,452	341	884	990	25.2	25.6	40.2	12	0.56	5.83	1.27

- <sup>a</sup> Normalized difference vegetation index.

## METHODS

During 2005–2014, we captured and radio-collared adult female elk from 9 populations in southwestern Montana on their winter ranges using helicopter net-gunning or chemical immobilization (Table 2). Elk populations were selected for capture and radio-collaring as part of several different projects related to carnivore-elk interactions, elk brucellosis, or elk survival investigations. In all cases, collared elk were selected randomly from those present on the winter ranges. Collar functionality differed among populations and years, and all collars contained global positioning system (GPS) receivers that collected 12–48 locations/day for a minimum of 1 year. Because our goal in this project was to synthesize data collected across a large spatial scale, we pooled data from these 9 elk populations to create a regional elk location dataset; we also used the individual population datasets. All animals were handled according to approved Institutional Animal Care and Use Committee protocols.

Table 2. Global positioning system location data collection and the number of collared elk in 9 southwest Montana, USA, elk populations

<b>Population</b>	<b>Yr</b>	<b>No. individuals included in the analysis</b>
Bitterroot East Fork	2011	23
	2012	18
	2013	16
Bitterroot West Fork	2011	9
	2012	15
	2013	18
Blacktail	2011	22
	2012	6
Dome Mountain	2007	11
	2008	27
Madison Valley	2005	17
	2006	24
Paradise Valley	2009	37
Pioneers	2013	28
Sage Creek	2012	16
	2013	3
Sapphires	2014	36

We developed separate archery- and rifle-season resource selection functions using a used-available framework (Johnson [1980](#), Manly et al. [2007](#)). Archery and rifle seasons for each year were defined by the Montana Fish, Wildlife, and Parks hunting season dates (Appendix S1, available online in Supporting Information). We treated locations collected from the GPS collars as the used sample. We randomly selected 4 used locations per individual per day to reduce spatial autocorrelation in the data (Hansteen et al. [1997](#)), to ensure that sample sizes were equal for all individuals regardless of collar scheduling, and to avoid potential bias in habitat use that can result from systematic data selection (e.g., collecting locations at 0000, 0600, 1200, 1800). The collars were designed to drop-off after 1 year; however, for a small number of individuals, the drop-off feature failed. To maintain equal sampling effort for all individuals, we used only data from the first year each individual was collared. For 5 of the populations, there were a small number of individuals ( $\leq 12$ /population) that had  $\geq 1$  day with  $< 4$  locations. In these cases, we used all available data for those days ( $< 4$  locations), thus underweighting those individuals in the models. We still included  $\geq 92\%$  of the possible locations for the period of interest for those individuals. We defined population-specific annual ranges by randomly selecting 1 location per day per individual to reduce spatial autocorrelation among the locations, and then building 99% kernel density estimator (KDE) contours using kernelUD in the adehabitat package in R, with the *ad hoc* smoothing method. We randomly generated available points at a 1:5 used:available ratio within the population-specific annual range, such that the available sample for each herd was drawn from within that herd's annual range (Northrup et al. [2013](#)).

We evaluated 9 covariates (Table 3) describing elk resource selection based on a review of previous elk studies and current metrics used for elk habitat management (Hillis et al. 1991, Christensen et al. 1993, Proffitt et al. 2011, McCorquodale 2013, Ranglack et al. 2016). To represent roads and other motorized routes, we included distance to motorized routes (McCorquodale 2013). In this case, we included only routes that were open to public motorized use during the hunting season. We excluded all other routes (private, administrative, or closed routes) because we were focused only on those routes and areas that would be accessible to public hunters. Private (on private land and access controlled by private landowners), administrative (gated forest roads available only to agency personnel for infrequent administrative use), and closed routes (routes that are closed to motorized use for all users) are also excluded when classifying security areas (MDFWP and USDA Forest Service 2013). To represent general landscape characteristics, we included 4 landscape attributes: canopy cover, slope, elevation, and solar radiation. Hunting pressure was represented using 2 covariates: accessible for public hunting (hunter access) and hunter effort. Hunter access was a binary covariate contrasting lands that were freely accessible to public hunters with lands that may restrict public hunter access. For the purposes of this analysis, we considered public lands that permitted hunting and private lands enrolled in the State of Montana's Block Management hunter access program to be publicly accessible, and considered all other lands restricted, though there was likely some unknown level of hunter pressure on most of these lands. We estimated hunter effort annually per hunting district using the Montana Fish, Wildlife and Parks harvest survey program, and created an index of hunter pressure for each hunting district as hunter days/km<sup>2</sup>, which we used for the archery and rifle seasons. During the archery season (Appendix S1), we included a remotely sensed metric of greenness derived from the normalized difference vegetation index (NDVI), time-integrated NDVI, to represent effects of nutritional resources on selection (Pettorelli et al. 2011). Time-integrated NDVI represents the net primary production during the growing season (Jonsson and Eklundh 2002, White et al. 2009), and is an important factor influencing summer elk resource selection in this area (Garrouette et al. 2016, Ranglack et al. 2016). During the rifle season (Appendix S1), we included snow water equivalent (SWE) as a covariate representing effects of snowpack on selection. We generated SWE values based on the maximum SWE value from the Snow Data Assimilation System (SNOWDAS; National Operational Hydrologic Remote Sensing Center 2004) for each pixel during each of 6 6-day periods during the rifle season (i.e., hunt period). These hunt periods were unique for each year. Full details on covariate development are included in Appendix S2, available online in Supporting Information.

Table 3. The covariates included in analysis of female elk archery season and rifle season resource selection in southwest Montana, USA, 2005–2014, with the spatial scales and the functional forms (linear, pseudothreshold, quadratic) or data type (binary) that we evaluated for each covariate

Covariate	Functional form(s)	Spatial scales (m)	Season(s)
Normalized difference vegetation index.			
Access	Binary	30	Both

Canopy cover	Pseudothreshold	30, 100, 250, 500, 750, 1,000	Both
Distance to motorized routes	Pseudothreshold	30	Both
Elevation	Quadratic	30, 100, 250, 500, 750, 1,000	Both
Hunter effort	Linear, pseudothreshold	Hunting unit	Both
Slope	Quadratic	30, 100, 250, 500, 750, 1,000	Both
Snow water equivalent	Linear, pseudothreshold	1,000	Rifle only
Solar radiation	Quadratic	30, 100, 250, 500, 750, 1,000	Both
Time-integrated NDVI <sup>a</sup>	Pseudothreshold	250, 500, 750, 1,000	Archery only
<ul style="list-style-type: none"> <li>• Normalized difference vegetation index.</li> </ul>			

Although resource selection analyses are typically conducted at the resolution of the available covariate data, animals may perceive and select resource attributes at different spatial scales (Anderson et al. [2005](#), DeVoe et al. [2015](#), Laforge et al. [2015](#)); therefore, we considered each continuous covariate over 6 different spatial scales (30, 100, 250, 500, 750, 1,000 m) using a moving window average with a search radius equal to the spatial scale, unless the resolution of the original data did not allow for analysis at certain spatial scales (Table [3](#)). Examining spatial scales is becoming increasingly important as remote sensing technology advances, leading to increasingly fine data resolutions, which may exceed the ability of individual animals to detect differences from one pixel to the next. Additionally, because the relationship between selection and covariates might be nonlinear, we evaluated multiple functional forms (linear, quadratic, pseudothreshold) for each continuous covariate. We fit pseudothreshold functional forms using a natural log transformation (Franklin et al. [2000](#)). We considered binary covariates only at the 30-m spatial scale because that was the scale of the original data. We evaluated spatial scale and functional forms for each covariate in an exploratory analysis, unless the most appropriate functional form could be identified *a priori* from existing literature (Table [3](#)).

We standardized all continuous covariates by subtracting the mean and dividing by 2 times the standard deviation prior to analysis (Gelman [2008](#), Lele [2009](#)). We used a multi-tiered approach to model selection (Franklin et al. [2000](#)) to reduce the number of competing models (Burnham and Anderson [2002](#)). We screened all continuous covariates for multi-collinearity using Pearson's correlation coefficients. We not included covariates that were collinear ( $|r| \geq 0.7$ ) with one another in the same model. In tier 1, we examined all possible univariate models in an exploratory analysis to determine the most explanatory functional form(s) and spatial scale(s) for each covariate. We ranked models using corrected Akaike's Information Criterion ( $AIC_c$ ) and advanced covariates from all the models within 5  $AIC_c$  units of the top model to the next tier. In the next tier, we combined the top covariate forms and scales in all possible combinations to

determine the overall best-supported model, according to  $AIC_c$ , for elk resource selection during the hunting seasons. We also included interactions between hunter access and distance to motorized routes, hunter access and canopy cover, distance to motorized routes and canopy cover, distance to motorized routes and time-integrated NDVI or SWE (archery or rifle), and distance to motorized routes and hunter effort. We removed uninformative covariates, if any, following recommendations made by Arnold (2010). We modeled resource selection separately for the archery and rifle seasons.

We pooled data from all herds and fit models using a conditional logistic regression model, conditioned on herd-year (unique for each population by yr combination) for the archery season to allow for the annually varying time-integrated NDVI values and herd-hunt period (unique for each population and hunt-period combination) for the rifle season to allow for the 6-day variation in SWE using `cph` in R version 3.2.2. We chose this modeling framework to ensure that the available points for each stratum were evaluated against the used points for that stratum, because there were time-varying covariates, a different set of instrumented individuals for each year, and different available choice sets for each population.

We then fit population-specific models using the same model structure as that found in the top pooled model to examine the functional response between the distance to motorized routes, canopy cover, hunter effort, and hunter access standardized coefficient estimates along gradients of accessible:restricted access lands and hunter pressure, because these varied among populations. We generalized least squares estimation using `gls` in the `nlme` package in R for the population-specific models. Because our dependent variables (standardized model coefficient estimates) were estimates with associated standard errors instead of measured values, we weighted each estimate by the inverse of the variance (Marin-Martinez and Sanchez-Meca 2009), such that estimates that were estimated with greater precision were given more weight than those that were estimated with less precision. We identified functional responses as significant if the 95% confidence intervals on the slope of the estimated regression lines did not overlap 0.

We then evaluated the relative support from the data for our resulting top models and models representing the traditional security area paradigm (Hillis et al. 1991, Christensen et al. 1993). To do so, we examined plots from our top models depicting how relative resource selection changed as canopy cover and distance to motorized routes increased across the range of available values for publicly accessible elk during each season while holding all other covariates at their means. From those, we identified the values of canopy cover and distance to motorized routes where relative resource selection begins to reach a pseudothreshold, which we arbitrarily defined as having a relative slope of 0.5 ( $\text{slope} = \text{range of Y values} / [2 \times \text{range of X values}]$ ). We considered these cutoff values to be analogous to the  $\geq 40\%$  canopy cover and  $\geq 0.8$ -km distance to motorized route commonly used in the traditional security area paradigm (Hillis et al. 1991, Christensen et al. 1993). To test the influence of block size on elk selection of areas with canopy cover and distance from motorized routes (attributes considered indicative of security areas), we varied the block size of our security area definitions to include areas  $\geq 0 \text{ km}^2$  (no size requirement),  $\geq 1.01 \text{ km}^2$ ,  $\geq 2.02 \text{ km}^2$ ,  $\geq 4.05 \text{ km}^2$ ,  $\geq 8.09 \text{ km}^2$ , and  $\geq 20.23 \text{ km}^2$ . We then generated new binary rasters of elk security areas for each season using those cutoff values from our top models as the input (maps comparing the top archery and rifle security metrics with the

traditional security area paradigm can be found in Appendix S3).

To evaluate the importance of the canopy cover component of traditional security metrics, we generated rasters representing traditional security areas with a range of canopy cover values ( $\geq 0\%$ ,  $\geq 10\%$ ,  $\geq 20\%$ ,  $\geq 30\%$ ,  $\geq 40\%$ ,  $\geq 50\%$ ,  $\geq 60\%$ ,  $\geq 70\%$ ), while holding the distance to route ( $\geq 0.8$  km) and size of the block ( $\geq 1.01$  km<sup>2</sup>) constant and compared models with this range of traditional security covariates. This resulted in 8 traditional security area metrics and 6 security area metrics derived from our analyses for each season.

To compare traditional security areas with those identified in our analyses, we extracted values for used and available points from our new security rasters and the traditional paradigm rasters with varying canopy cover. We then fit our top model for each season, replacing the canopy cover and distance to motorized routes covariates with either the traditional security area paradigm with varying canopy cover or our new security area values. We compared these models using AIC<sub>c</sub> to determine which combination of canopy cover, distance to motorized routes, and block size covariates was most supported by the data.

Lastly, to determine whether the proportion of security areas within a population home range influenced the extent to which the population redistributed from publicly accessible to restricted access lands through the course of the fall hunting season, we examined a potential relationship between elk redistribution and the proportion of the annual range qualified as a security area, using linear regression. We quantified redistribution as the difference between the proportion of used locations on publicly accessible lands in August and the proportion of used locations on publicly accessible lands during the rifle season for each population. The proportion of the population annual range defined as a security area was based only on the publicly accessible portion of the annual range, and was calculated based on the security area metrics from our top archery and rifle models, and using the traditional security area definition that included 40% canopy cover.

## RESULTS

We used 57,282 archery season and 47,602 rifle season elk locations collected from 325 individual elk in our analyses. Of the used locations, 61.9% and 52.5% occurred on publicly accessible lands during the archery and rifle seasons, respectively. Mean elevation of used points was  $2,104 \pm 463$  (SD) m and  $2,005 \pm 420$  m during the archery and rifle seasons, respectively. Mean distance to motorized routes of used points was  $2,586 \pm 2,982$  m and  $2,058 \pm 2,109$  m during the archery and rifle seasons, respectively. Mean time-integrated NDVI of used points during the archery season was  $52.6 \pm 11.6$ . Mean SWE of used points during the rifle season was  $27.7 \pm 28.8$  mm. The mean slope of the used points was  $14.3 \pm 9.4$  degrees and  $14.1 \pm 8.9$  degrees during the archery and rifle seasons, respectively. The mean canopy cover of the used points was  $27.7 \pm 25.2\%$  and  $19.6 \pm 23.2\%$  for the archery and rifle seasons, respectively.

### Elk Resource Selection

Using the pooled regional dataset, the full model was the most supported model of elk resource

selection during the archery hunting season, with the next best model having a  $\Delta AIC_c = 80.4$ . In general, elk were more likely to use areas that restricted public access. Regardless of accessibility, elk were less likely to use hunting districts with higher hunter effort. Further, elk were more likely to use areas as distance to motorized routes, canopy cover, time-integrated NDVI, and solar radiation increased, though distance to motorized routes and canopy cover quickly reached a pseudothreshold at  $\geq 2,760$  m and  $\geq 13\%$ , respectively, for publicly accessible lands. Elk used moderate slopes as compared to flat or steeper slopes (Fig. 2 and Table 4). All interactions improved model fit. Model results indicated that elk were more likely to use areas with higher canopy cover at all distances from motorized routes and were more likely to use areas far from motorized routes at all levels of canopy cover. At high NDVI values, there was little difference in elk selection for areas near versus far from motorized routes, but at low NDVI values, elk were more likely to use areas far from motorized routes. Elk also were less likely to use areas with higher hunter effort if they were closer to motorized routes, but elk showed little response to increases in hunter effort far from motorized routes. Additionally, the difference in strength of selection for areas with high and low canopy cover were greater on publicly accessible lands than on lands that restricted access. This same pattern was also found for the difference in the strength of selection for areas near and far from motorized routes (Fig. 3 and Table 4, Appendix S4).

Using the pooled regional dataset, the full model was the most supported model of elk resource selection during the rifle hunting season, with the next best model having a  $\Delta AIC_c = 36.6$ . Similar to the archery hunting season model, elk were more likely to use areas that restricted public access during the rifle season. Regardless of accessibility, elk were more likely to use areas as distance to motorized routes, canopy cover, hunter effort, and solar radiation increased, and less likely to use areas as elevation and SWE increased. Elk responses to distance to motorized routes, canopy cover, and hunter effort quickly reached pseudothresholds at  $\geq 1,535$  m,  $\geq 9\%$ , and  $\geq 1.33$  hunter days/km<sup>2</sup>, respectively, for publicly accessible lands. Elk also were more likely to use moderate slopes (Fig. 4 and Table 4). All of the interactions improved model fit. Elk showed a stronger response to increases in SWE when far from motorized routes than when near motorized routes. Elk showed stronger selection for areas farther from motorized routes in areas with high hunter effort, whereas they showed little response to increases in hunter effort when near motorized routes. Similar to the archery season, the difference in strength of selection for areas with high and low canopy cover were greater on publicly accessible lands than on lands that restricted public access. However, contrary to the archery season results, the difference in the strength of selection for areas near and far from motorized routes was greater in areas that restricted access (Fig. 5 and Table 4, Appendix S4).

In our functional response analysis, we detected no changes in the strength of selection for areas that had higher canopy cover, restricted public access, or lower hunter effort with increases in the ratio of accessible:restricted access lands and hunter effort during the archery and rifle seasons (Table 5, Appendix S5). However, elk were significantly more likely to use areas farther from motorized routes as mean hunter effort in the annual range increased during the archery (Fig. 6a) and rifle seasons (Fig. 6b). This response was very similar during the rifle season ( $0.20 \pm 0.09$ , estimate  $\pm$  SE) and the archery season ( $0.19 \pm 0.07$ ).

Table 5. The estimated regression slope (and SE) examining potential functional responses between the standardized coefficient estimates from the population-specific models for hunter access, canopy cover, distance to motorized routes, and hunter effort along gradients of accessible:restricted access and mean hunter effort for elk population annual ranges, southwestern Montana, USA, 2005–2014. Values with confidence intervals that do not overlap 0 are indicated with an asterisk

Covariate	Archery		Rifle	
	Accessible:restricted access	hunter effort	Accessible:restricted access	hunter effort
Hunter access	1.23 (1.06)	0.02 (0.10)	−0.02 (1.03)	−0.10 (0.10)
Canopy cover	0.79 (0.82)	0.11 (0.07)	0.42 (1.00)	0.11 (0.10)
Distance to motorized routes	1.06 (0.68)	0.19 (0.07)*	0.81 (0.75)	0.20 (0.09)*
Hunter effort	−1.09 (0.56)	−0.01 (0.08)	−0.06 (0.94)	0.06 (0.10)

## Security Areas

Based on the top model from the archery season, we identified areas with  $\geq 13\%$  canopy cover (1,000-m spatial scale) and  $\geq 2,760$  m from a motorized route as security areas for elk during the archery season. The model including these 2 parameters, without a defined minimum block size ( $\geq 0$  km<sup>2</sup>), received the most support, with the next best model having a  $\Delta AIC_c = 88.9$  (Table 6). All of the new security area metrics arising from our most supported archery season model were more strongly supported than all of the traditional security area metrics. Of the traditional security area metrics with a minimum block size of 1.01 km<sup>2</sup>  $\geq 0.80$  km from a motorized route,  $\geq 10\%$  canopy cover was the most supported (Table 6).

Table 6. Comparison of the traditional security habitat paradigm based on  $\geq 0.80$  km from a motorized route,  $\geq 1.01$ -km<sup>2</sup> block size, and canopy cover varying from  $\geq 0$ –70% in increments of 10% and security area definitions based on results of the top ranked model and 6 different minimum block sizes ( $\geq 0$ , 1.01, 2.02, 4.05, 8.09, and 20.23 km<sup>2</sup>) for each elk hunting season, southwestern Montana, USA, 2005–2014. During the archery season, the top model defined secure areas based on  $\geq 13\%$  canopy cover (1,000-m spatial scale),  $\geq 2,760$  m from a motorized route. During the rifle season, the top model defined secure areas based on  $\geq 9\%$  canopy cover (1,000-m spatial scale),  $\geq 1,535$  m from a motorized route

Model rank	Archery		Rifle	
	Model	$\Delta AIC_c$ <sup>a</sup>	Model	$\Delta AIC_c$
1	Archery $\geq 0$ km <sup>2</sup>	0.0	Rifle $\geq 20.23$ km <sup>2</sup>	0.0

<sup>a</sup> Corrected Akaike's Information Criterion.

2	Archery $\geq 1.01 \text{ km}^2$	88.9	Rifle $\geq 0 \text{ km}^2$	24.7
3	Archery $\geq 2.02 \text{ km}^2$	94.0	Rifle $\geq 2.02 \text{ km}^2$	66.3
4	Archery $\geq 4.05 \text{ km}^2$	138.2	Rifle $\geq 1.01 \text{ km}^2$	90.4
5	Archery $\geq 8.09 \text{ km}^2$	167.0	Rifle $\geq 4.05 \text{ km}^2$	105.0
6	Archery $\geq 20.23 \text{ km}^2$	229.7	Rifle $\geq 8.09 \text{ km}^2$	151.6
7	Traditional $\geq 10\%$ canopy	482.2	Traditional $\geq 0\%$ canopy	266.3
8	Traditional $\geq 0\%$ canopy	781.7	Traditional $\geq 10\%$ canopy	1,327.1
9	Traditional $\geq 20\%$ canopy	1,088.0	Traditional $\geq 20\%$ canopy	1,699.7
10	Traditional $\geq 30\%$ canopy	1,208.4	Traditional $\geq 30\%$ canopy	1,767.2
11	Traditional $\geq 40\%$ canopy	1,407.5	Traditional $\geq 40\%$ canopy	1,988.1
12	Traditional $\geq 50\%$ canopy	1,843.8	Traditional $\geq 50\%$ canopy	2,491.7
13	Traditional $\geq 60\%$ canopy	2,049.3	Traditional $\geq 70\%$ canopy	3,214.8
14	Traditional $\geq 70\%$ canopy	2,691.1	Traditional $\geq 60\%$ canopy	3,229.7

Based on the top model from the rifle season, we identified areas with  $\geq 9\%$  canopy cover (1,000-m spatial scale) and  $\geq 1,535 \text{ m}$  from a motorized route as security areas for elk during the rifle season. The model including these 2 parameters with a minimum block sizes of  $20.23 \text{ km}^2$  received the most support, with the next best model having a  $\Delta\text{AIC}_c = 24.7$  (Table 6). Similar to the archery season models, all of the new security area metrics derived from our most supported rifle season model were more strongly supported than all the traditional security area metrics. Of the traditional security area metrics with a minimum block size of  $1.01 \text{ km}^2$   $\geq 0.80 \text{ km}$  from a motorized route,  $\geq 0\%$  canopy cover was the most supported (Table 6). We did not detect any relationships between the amount of elk redistribution from accessible to restricted access lands and the proportion of the annual range in any of the security area metrics.

## DISCUSSION

Overall, our results suggest that elk habitat management during hunting seasons should focus on hunter access, hunter effort, canopy cover, and motorized routes. These covariates all had important effects on elk resource selection during the archery and rifle seasons and are under some degree of management control. Additionally, nutritional resources are important influences of female elk resource selection during the archery hunting season and should be considered in elk hunting season habitat management strategies. Depending on population size objectives (increase or decrease elk population size) managers can attempt to manipulate each of these factors to make elk more or less vulnerable to harvest. However, managers should also consider that increases in hunter effort (particularly during the rifle season) or motorized routes may encourage elk to select for areas that restrict public hunter access and result in a redistribution of elk away from public lands. We also recommend that new security area metrics derived from our most supported models be considered (Table 6). Because these metrics are predictive of elk resource selection, they may encourage elk to remain on publicly accessible lands throughout the hunting seasons, enabling sufficient harvest to affect population growth rate and providing season-long hunter opportunities on public land.

Our modeling of female elk resource selection during the archery and rifle hunting seasons suggests that, in general, female elk have similar resource selection patterns in both seasons, particularly in relation to factors over which managers have some level of control (distance to motorized routes, canopy cover, and hunter access). Lands that restricted access to hunters were preferred to publicly accessible lands during both seasons. Thus, we recommend that managers work closely with private landowners to increase public accessibility to private lands if management goals are to reduce elk population size. Additionally, the results of our functional response analysis suggest that high hunter effort during the archery season increases elk avoidance of areas near motorized routes (Fig. 6a) in a similar manner to elk responses during the rifle season (Fig. 6b). We recommend managers consider wildlife related motorized travel closure dates that include archery and rifle season in areas of high hunter effort, or hunting seasons that limit hunter effort in areas of high motorized route densities to maintain elk distribution on publicly accessible lands.

The increase in elk selection for areas farther from motorized routes with increases in hunter effort (Fig. 6) helps to explain the documented shift in elk movements during archery hunting seasons that occur in some areas (Conner et al. 2001, Vieira et al. 2003). Contrary to Vieira et al. (2003), we found that hunter effort influenced elk resource selection during the archery season; elk generally avoided areas of high hunter effort, with this response being stronger in areas near motorized routes. In our study sites, this selection pattern also involves elk selecting for lands that restricted access, which had one of the strongest effects on elk resource selection during the archery season. Security for elk on publicly accessible lands has traditionally been regarded as areas away from motorized routes with high canopy cover that can maintain elk even during periods of hunting stress (Lyon 1979, 1983; Hillis et al. 1991). Hunter access had a stronger influence on elk resource selection in both hunting seasons than either distance to motorized routes or canopy cover (Table 4).

The influence of late-summer nutrition on ungulate population dynamics and resource selection has been documented (Cook et al. 2004, 2013; Monteith et al. 2014; Ranglack et al. 2016), but the potential effects of nutrition on archery season elk distributions have not been previously evaluated. Using data from these same study areas, Ranglack et al. (2016) reported that during July and August, female elk selected strongly for areas of high nutritional resources (as represented by time-integrated NDVI), but that motorized routes had a relatively small influence on selection. Using standardized coefficient estimates to compare summer and archery season effects in the same 9 elk herds, female elk avoidance of motorized routes nearly doubled during the archery season, whereas selection for areas with higher time-integrated NDVI values decreased by nearly half. Our results suggest that during the archery hunting season, female elk continue to seek out areas of high nutritional value, even when they are near motorized routes (Fig. 3), but this selection has been reduced, likely because of the increased avoidance of motorized routes or selection for the other covariates that we documented as influential. If elk attempt to select for areas of high nutritional value throughout the archery hunting season but are unable to do so because of hunting risk, archery hunter pressure may compromise female nutritional status at a critical time of year (Noyes et al. 2004, Davidson et al. 2012). This suggests that archery hunting has the potential to affect fall nutritional condition of female elk, and potentially pregnancy rates and body fat levels of elk entering the winter season. This topic needs more investigation and managers may need to consider including motorized route closures,

earlier closure dates during travel planning, and limits on hunter numbers during the archery season in areas of high nutritional value for elk if maintaining elk access to nutritional resources is part of the management intention.

During the rifle season, elk avoided areas near motorized routes and the response was stronger than during the archery season, indicating that the impact of motorized routes on elk resource selection continues to increase from summer (Ranglack et al. [2016](#)) to archery and rifle seasons. Although not unexpected given the vast literature on road effects on ungulates (McCorquodale [2013](#)), these differences suggest that elk response to motorized routes varies seasonally and is strongly related to the risks associated with hunting seasons. Based on the thresholds we identified in our most supported models, during the archery season, we recommend managing for areas  $\geq 2,760$  m from the nearest motorized route; this distance decreases during the rifle season to  $\geq 1,535$  m. This indicates that although the overall influence of motorized routes on elk resource selection during the archery season is lower than during the rifle season, the spatial scale of effects during archery season is larger. This may be because archery hunters are more apt to hike farther away from motorized routes in pursuit of elk. In contrast, rifle hunters have a stronger but more limited area of influence around motorized routes. The impact of motorized routes on elk resource selection during the hunting seasons is further supported by the functional response depicting increasing selection for areas farther from motorized routes with higher hunter effort (Fig. [6](#)). Given the increasing popularity of archery hunting, the different impacts of archery and rifle hunters should be incorporated into management by extending motorized route closures such that they include the archery season (MDFWP and USDA Forest Service [2013](#)). Additionally, because of the larger spatial influence of motorized routes during the archery season, some motorized routes may warrant closure during the archery season only and can be re-opened during the rifle hunting season.

Overall, we saw very similar patterns of resource selection during the archery and rifle hunting seasons, in terms of direction of selection for the different covariates but also for the spatial scale of each covariate that received the most support from the data. However, the direction of selection for hunter effort changed from the archery to rifle season (Table [4](#)), possibly because of the impacts of snow during the rifle season. Snow accumulation is strongly associated with the ecology and behavior of animals in cold climates because snow can reduce access to forage patches (Craighead et al. [1973](#), Bruggeman [2006](#)) and increase energy expenditure for thermoregulation, travel, and search for food (Parker et al. [1984](#), Telfer and Kelsall [1984](#)). We found the influence of SWE on elk resource selection to be moderated by distance to motorized routes, with elk showing stronger responses to increases in SWE when far from motorized routes than when near motorized routes (Fig. [5](#)). This indicates that when near routes, elk are balancing searching for areas of low SWE with other factors. During the archery season, when elk are not limited by snow and the effect of motorized routes is weaker, elk are more likely to use areas with lower hunter effort. However, during the rifle season, elk are more limited in the habitats that are available to them because of snow accumulation. Hunters may in turn respond to these more tightly defined elk resource selection patterns, making it appear that elk are more likely to be found in areas of high hunter effort when in reality hunter effort may be higher where elk are more likely to be present.

The traditional security paradigm of managing for blocks of unfragmented forest cover away


from motorized routes (Lyon [1979](#), [1983](#); Hillis et al. [1991](#)) has been widely accepted and is likely a factor contributing to increasing elk populations over the last 50 years (Lonner and Cada [1982](#), Hillis et al. [1991](#), Picton [1991](#), O'Gara and Dundas [2002](#)). Our results suggest that similar security paradigms could be applied to southwestern Montana in efforts to encourage female elk to use public lands. During the archery season, our analysis suggests that areas with  $\geq 13\%$  canopy cover (1,000-m scale) that are  $\geq 2,760$  m from the nearest motorized route may be perceived by female elk as secure, regardless of block size. During the rifle season, areas with  $\geq 9\%$  canopy cover, that are  $\geq 1,535$  m from the nearest motorized route, with a block size of  $\geq 20.23$  km<sup>2</sup> may be perceived by female elk as secure. This, along with our analysis of the traditional paradigm with varying levels of canopy cover (Table [6](#)), suggests that the often used 40% canopy cover threshold for security areas is too stringent, and that the influence of motorized routes is more important than canopy cover to female elk resource selection. Indeed, our models show that although important initially, the influence of canopy cover on elk resource selection reaches pseudothresholds at relatively low values for both hunting seasons. We found that for the archery season no minimum block size requirement was supported by our data, whereas the largest minimum block size we tested (20.23 km<sup>2</sup>) was required during the rifle season. This pattern perhaps reflects the generally higher hunter pressure and harvest during the rifle season than the archery season, leading to a need for large security areas.

Although it may be beneficial to increase the proportion of security areas within population annual ranges, we found no relationship between the proportion of security areas within the annual range and the amount of redistribution that occurs in these elk populations. This highlights that even when security areas are available on publicly accessible lands, elk may still choose to redistribute to lands that restrict access. This may be due to learned behaviors that are passed from one generation to the next (Boyce [1991](#)), refuge from hunting risk on lands that restrict access, or other unmeasured factors. In any case, this result highlights the importance of state and federal wildlife and land management agencies working collaboratively with private landowners.

## MANAGEMENT IMPLICATIONS

We recommend that managers manage for areas with  $\geq 13\%$  canopy cover that are  $\geq 2,760$  m from a motorized route during the archery season to maintain elk distribution on publicly accessible lands during archery and rifle seasons. Special attention should also be given to areas of high nutritional resources during the archery season, as this is an important nutritional period that may affect elk population dynamics (Noyes et al. [2004](#), Davidson et al. [2012](#)). During the rifle season, we recommend management for areas with  $\geq 9\%$  canopy cover that are  $\geq 1,535$  m from a motorized route, and are  $\geq 20.23$  km<sup>2</sup>. However, elk may continue to use restricted access lands as a result of the strong hunting refuge they provide and learned behavior (MDFWP and USDA Forest Service [2013](#)). Given the strength of selection for areas that restricted access to public hunters in both seasons, we recommend managers work closely with private landowners to increase public accessibility to private lands if management goals are to reduce elk population size, while considering the amount of hunter pressure and motorized routes in the elk populations they are managing. Lastly, given the functional response between distance to motorized routes and hunter effort, we recommend that managers consider wildlife-related travel closure dates to include both archery and rifle seasons in areas of high hunter pressure, or

hunting seasons that limit hunter pressure in areas of high motorized route densities.

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